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SIZE VARIATION IN FOOT ELEMENTS OF *BISON* FROM RANCHO LA BREA¹

By Wade E. Miller² and Jack D. Brotherson³

ABSTRACT: Measurements, in the form of statistical summaries, are given for the foot elements of all available specimens of *Bison antiquus* and *Bison ? latifrons* from the Rancho La Brea collection at the Natural History Museum of Los Angeles County. These elements show only moderate variability in measurements, and variability in morphology seems generally slight. Sexual dimorphism appears in only the metacarpal. Rare *Bison ? latifrons*' metapodials can possibly, but not easily, be distinguished from those of *B. antiquus*.

INTRODUCTION

Foot bones probably represent the most commonly recovered bison fossils in Rancho La Brea; therefore, it is desirable to furnish data on one of the largest known collections. This paper provides data on the size variability for a very large sample of foot elements of *Bison antiquus* (recognized as *B. bison antiquus* by Flerov 1967) as well as limited information on *B. ? latifrons*. Foot bones studied include carpals, tarsals, metacarpals, metatarsals and phalanges of both front and hind feet. The carpal, tarsal, metapodial and phalanx data are summarized in Table 1. All available specimens from the Rancho La Brea collection at the Natural History Museum of Los Angeles County were used in the present study.

Although the Rancho La Brea fauna has been known for many years, only a few of its taxa have actually been thoroughly studied. The bison included in this fauna are mentioned in numerous scientific articles, including the general Rancho La Brea faunal paper by Stock (1968), but a comprehensive study has not yet been made. Miller (1971) gave measurements of a few Rancho La Brea bison skeletal elements, including some foot bones, in comparison with bison from Costeau Pit in southern California.

The Rancho La Brea sample of *Bison antiquus* ranks among the largest assemblages of fossil *Bison* from any presently described locality. Skinner and Kaisen (1947, p.131) discussed the Alaskan collections of bison in which over 1,200 individuals are present. However, many different sites were evidently involved and four species were included. Skinner and Kaisen did not separate these species in their tables for Alaskan fossil bison metapodials, the only postcranial bones they measured.

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tory Museum of Los Angeles County, for permission to study the bison material presented in this paper. The senior author enlisted the aid of Dr. Jack D. Brotherson as biometrician and co-author. Appreciation for assistance in mathematical computations is extended to Mr. Gary Heaston of Brigham Young University. Miss Jill Olsen of Brigham Young University drew figures of the foot bones.

METHODS

With the exception of sesamoids, all available foot bones of bison (carpals, tarsals, metapodials and phalanges) from the Rancho La Brea fauna at the Natural History Museum of Los Angeles County were studied. 2,756 bones representing all 15 foot elements were measured and are statistically summarized in Table 1 (individual measurements taken for each bone, which includes specimen number, pit number from which specimens were obtained and depths of recovery, are not given here due to bulk, but they are currently on file in the Earth Sciences Division at the above museum). Figures 10 through 24 show precisely where each measurement was taken. Only adult specimens were considered in this study. Epiphyseal fusion, definition of processes and bone density were used in determination of maturity.

Means, standard deviations and coefficients of variation (Ostle 1963) were computed on all measurements taken (Table 1). Histograms (Figs. 1 and 2) and scatter diagrams (Figs. 3-9) were

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constructed for metacarpals and metatarsals as these bones permitted the greatest possible absolute disparity in measurements and might most readily reflect sexual dimorphism and/or presence of more than one species. The Kolmogorov-Smirnoff test (Ostle 1963) was run on these elements in order to determine whether normality in distribution patterns existed. Should they occur in the Rancho La Brea fauna, *Bison latifrons*' metapodials would presumably be among the longest and almost certainly would be the most robust. Correlation analysis (Ostle 1963) was employed in order to determine which combination of metapodial measurements (Table 2) would be most ideal in constructing the scatter diagrams (some elements have identical coordinates in these diagrams but have been shown as contiguous dots for discernment). Discriminant analysis (Klecka 1975) was used to ascertain whether the bones thought to represent a second species could be independently classified. An S-360 Mod. 65 I.B.M. computer was used in both correlation and discriminant analysis.

RESULTS AND DISCUSSION

Visual inspection of the 2,756 bison foot bones examined showed only minor morphologic variations, mostly in the shapes of articular surfaces and processes. According to Skinner and Kaisen (1947, p. 134-135), isolated *Bison* metapodials can be sexed on the relative heaviness of shafts. However, sexual dimorphism is not clearly evident on this basis as seen in figures 3 through 9. It may be present in the metacarpals as evinced in the bimodal length distribution (Fig. 1) but not in metatarsals (Fig. 2). The Kolmogorov-Smirnoff test (Ostle 1963) was run on all specimens included in these two figures at the 0.01 significance level. It showed a condition of normality for the distribution of metatarsals but one of non-normality for the metacarpals. Male bison might have been relatively larger in their forequarters than females to present a more formidable image when facing any threat, intraspecific or otherwise. According to Guthrie (1970, p. 10), bison, presumably only males, use a frontolateral display when confronting other members of the species in an attempt to intimidate. This could help account for sexual dimorphism appearing in the metacarpals but not in the metatarsals. One disturbing factor in the supposed sexual dimorphism of the metacarpals is the ratio between males and females. Males, as interpreted from the histogram (Fig. 1), are approximately three-fourths as abundant as females. Thirty eight complete and partial skulls in the Rancho La Brea collection at the Natural History Museum of Los Angeles County indicate that males are less than half as abundant as females, 11 to 27. If the interpretation of the above histogram is correct, the discrepancy in the male-female ratio between metacarpals and skulls might be due to the relatively small sample size of the skulls, an unknown bias in the accumulation of the respective elements, or bias in the selection of skulls for loans or exchanges with other institutions. The male-female ratio in herds of the Recent bison is not given in most published literature. Also, statements conflict as to the composition of small bands which comprise or comprised major herds. For example Allen (1876, p. 57) stated that at no time of the year did the sexes form separate herds, while Mc Hugh (1972, p. 156-157) and Meagher (1973, p. 46) both reported that they did. The only known sex ratios on bison are from modern herds. Meagher (1973, p. 56-60) related that in the Yellowstone population, which has been left in a wild state since

the 1930's, the male-female ratio is variable depending upon age. She reported that there are more males than females in some age groups, while the reverse is true for others; with females slightly exceeding males in the overall population. Mr. Kendall Nelson (1976, personal communication), of the Utah Wildlife Division, indicated that the small state herd of bison (now about 200 individuals) has a sex ratio of 1.2 cows per bull. This herd has been left in a wild condition since its introduction into Utah in the 1940's. The sex ratio interpreted from Rancho La Brea *Bison* metacarpals is roughly similar to that found in living herds of bison.

A complicating factor in the present study is the possible inclusion of *Bison latifrons*' foot elements. As previously reported (Wyman 1926; Miller 1968), this giant bison existed as a rare component of the Rancho La Brea fauna. Schultz and Hillerud (1977) evidently did not accept the possibility of *Bison latifrons*' presence at Rancho La Brea. They commented (p. 104) on Miller reporting (1968) this species from the Rancho La Brea fauna and stated that the specimens were probably large *B. antiquus*, similar to *B. antiquus barbouri*. However, they did not mention Wyman's report (1926) of a *B. latifrons*' skull from Rancho La Brea which had a six foot horn core spread. Also, Miller gave (1971) additional information on the probability of *Bison latifrons* from Rancho La Brea to which Schultz and Hillerud made no reference. The presence of *B. latifrons* at Rancho La Brea is further strengthened by LACM HC 6013, a distal horn core fragment, which has not previously been reported. This fragment, which measures 233 mm along its outer curvature, falls within the variation noted for *B. latifrons* but not *B. antiquus*. Recorded data indicate that this specimen was recovered from pit 4 between 11 and 12 feet below ground level. Unpublished radio-carbon dates for pit 4 on file at the Natural History Museum of Los Angeles County indicate a time range from approximately 13,000 years B.P. to 35,000 years B.P. based on both wood and collagen. The depths from which dated *Bison ?latifrons* samples were collected range from 5 to 23.5 feet. The scatter diagrams given in this paper (Figs. 3-9) show a few individuals, indicated by lettered dots, which may represent this species. Surprisingly, the presumed *B. ?latifrons*' metapodials are not the longest ones. Discriminant analysis showed, however, that they can be classified as a distinct group. This analysis revealed that 100% of both the metacarpals and metatarsals of possible *Bison latifrons* were properly grouped as shown by the scatter diagrams. It also showed that the groupings of *B. antiquus*' metacarpals and metatarsals were, respectively, 97% and 89% correctly placed (Table 2 gives means and standard deviations for metapodial measurements relating to these two bison groups). the discriminant analysis further verified the importance of some metapodial parameters over others in distinguishing *B. antiquus* from *B. latifrons*. The most discriminating measurements for the metacarpals in order of importance are: greatest transverse width of distal end, least anteroposterior width of shaft, least transverse width of shaft and greatest transverse width of proximal end; and for the metatarsals, greatest transverse width of distal end, greatest length, greatest anteroposterior width of proximal end and greatest anteroposterior width of distal end. All the above parameters were shown to be significant at the 0.01 level. Carpals, tarsals and phalanges, because of smaller disparity in measurements, apparently do not allow distinctions to be made between *Bison latifrons* and *B. antiquus*.

A major purpose of this study is to provide a basic data base

which will show proportions as well as size. This will become more significant with the planned study of additional bison postcranial elements from Rancho La Brea. Previously it was suggested (Miller 1971, p. 29) that the body proportions of *Bison antiquus* differed from those of *B. ? latifrons*. Further research still needs to be done to confirm this, although some proportions of the metapodials do suggest distinctions as noted above. Examples of proportional body differences exist among modern bison species, as the European bison (the wisent), *B. bonasus*, is distinctly longer limbed and has a larger pelvis than the more massive American form, *B. bison*.

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TABLE 1
Statistical summary of *Bison* foot elements from Rancho La Brea (in mm).

	N	OR	X	s	s/X	s-X
METACARPAL	76					
1. Greatest length		205-235	221.22	7.02	0.03	0.81
2. Greatest anteroposterior width of proximal end		39-57	45.00	2.85	0.06	0.33
3. Greatest transverse width of proximal end		65-94	76.99	4.95	0.06	0.57
4. Least anteroposterior width of shaft		27-36	30.24	1.57	0.05	0.18
5. Least transverse width of shaft		38-59	47.59	3.41	0.07	0.39
6. Greatest anteroposterior width of distal end		37-49	42.69	2.27	0.05	0.26
7. Greatest transverse width of distal end		70-94	79.03	4.78	0.06	0.55
CALCANEUM	80					
1. Greatest length		155-201	173.21	7.77	0.04	0.87
2. Greatest height across sustentacular facet		59-75	65.79	3.55	0.05	0.40
3. Greatest overall height		64-76	68.88	3.40	0.05	0.38
ASTRAGALUS	143					
1. Greatest length		80-97	88.15	3.79	0.04	0.32
2. Greatest transverse diameter		50-67	58.06	3.31	0.06	0.28
3. Greatest anteroposterior diameter		46-59	50.47	2.52	0.05	0.21
NAVICULAR-CUBOID	146					
1. Greatest anteroposterior diameter		62-82	70.27	3.76	0.05	0.31
2. Greatest transverse diameter		64-85	72.01	4.07	0.06	0.34
3. Greatest height		52-77	63.76	4.10	0.06	0.34
MESO-ECTOCUNEIFORM	101					
1. Greatest anteroposterior diameter		42-54	47.65	2.55	0.05	0.25
2. Greatest transverse diameter		26-37	30.79	1.88	0.06	0.19
3. Greatest height		18-25	19.93	1.38	0.07	0.14
PISIFORM	67					
1. Greatest anteroposterior diameter		30-42	35.06	2.16	0.06	0.26
2. Greatest transverse diameter		20-31	23.81	2.36	0.10	0.29
3. Greatest height		31-42	34.28	2.26	0.07	0.28
CUNEIFORM	113					
1. Greatest anteroposterior diameter		27-40	31.90	2.83	0.09	0.27
2. Greatest transverse diameter		47-65	54.88	3.45	0.06	0.32
3. Greatest height		37-56	45.13	3.84	0.09	0.36
LUNAR	158					
1. Greatest anteroposterior diameter		50-71	57.51	3.74	0.07	0.30
2. Greatest transverse diameter		34-46	38.56	2.42	0.06	0.19
3. Greatest height		35-51	40.94	2.87	0.07	0.23
SCAPHOID	125					
1. Greatest anteroposterior diameter		50-68	56.33	3.73	0.07	0.33
2. Greatest transverse diameter		30-44	35.35	2.68	0.08	0.24
3. Greatest height		36-50	40.58	2.72	0.07	0.24
UNCIFORM	109					
1. Greatest anteroposterior diameter		36-51	42.18	2.86	0.07	0.27
2. Greatest transverse diameter		35-47	39.40	2.50	0.06	0.24
3. Greatest height		28-36	31.70	1.81	0.06	0.17

MAGNUM	126					
1. Greatest anteroposterior diameter		40-52	45.29	2.59	0.06	0.23
2. Greatest transverse diameter		42-60	48.47	3.50	0.07	0.31
3. Greatest height		25-33	28.14	1.74	0.06	0.16
METATARSAL	64					
1. Greatest length		258-287	271.45	6.71	0.02	0.84
2. Greatest anteroposterior width of proximal end		54-74	61.30	3.76	0.06	0.47
3. Greatest transverse width of proximal end		55-68	60.58	3.16	0.05	0.39
4. Least anteroposterior width of shaft		34-40	36.00	1.58	0.04	0.20
5. Least transverse width of shaft		33-48	39.34	2.95	0.07	0.37
6. Greatest anteroposterior width of distal end		39-49	43.11	2.01	0.05	0.25
7. Greatest transverse width of distal end		67-83	73.03	3.70	0.05	0.46
ANTERIOR PROXIMAL PHALANX	282					
1. Greatest length		63-82	72.60	5.22	0.07	0.31
2. Greatest anteroposterior diameter		37-51	43.02	3.17	0.07	0.19
3. Greatest transverse diameter		36-48	41.62	2.48	0.06	0.15
POSTERIOR PROXIMAL PHALANX	279					
1. Greatest length		64-85	74.95	3.46	0.05	0.21
2. Greatest anteroposterior diameter		36-48	41.43	2.21	0.05	0.13
3. Greatest transverse diameter		30-49	36.94	2.33	0.06	0.14
MEDIAL PHALANX	555					
1. Greatest length		43-60	49.94	2.93	0.06	0.12
2. Greatest anteroposterior diameter		30-49	38.69	2.98	0.08	0.13
3. Greatest transverse diameter		30-50	38.57	3.29	0.09	0.14
UNGUAL PHALANX	337					
1. Greatest length		70-101	85.65	6.14	0.07	0.33
2. Greatest transverse diameter		27-41	33.15	2.60	0.08	0.14

Points of measurement shown in Figures 10-24

N = number of specimens s = standard deviation
OR = observed range s/X = coefficient of variation
X = mean s-X = standard deviation of the mean

TABLE 2
Means and standard deviations of *Bison antiquus* and *Bison ? latifrons* metapodials from Rancho La Brea (in mm).

	METACARPALS					
	<i>Bison antiquus</i>			<i>Bison ? latifrons</i>		
	N	X	s	N	X	s
1. Greatest length	69	220.51	6.79	7	228.28	5.41
2. Greatest anteroposterior width of proximal end		44.59	2.40		49.00	3.96
3. Greatest transverse width of proximal end		76.07	4.01		86.00	4.51
4. Least anteroposterior width of shaft		29.94	1.12		33.14	1.86
5. Least transverse width of shaft		46.94	2.71		54.00	3.00
6. Greatest anteroposterior width of distal end		41.65	5.41		46.86	1.35
7. Greatest transverse width of distal end		78.06	3.59		88.57	4.72

	METATARSALS					
	59			5		
1. Greatest length		271.41	6.82		271.45	6.28
2. Greatest anteroposterior width of proximal end		60.69	3.21		67.17	3.92
3. Greatest transverse width of proximal end		60.10	2.81		65.17	2.72
4. Least anteroposterior width of shaft		35.90	1.59		37.00	1.26
5. Least transverse width of shaft		38.93	2.52		43.33	3.98
6. Greatest anteroposterior width of distal end		42.95	2.00		44.67	2.01
7. Greatest transverse width of distal end		72.34	2.81		79.67	3.70

N = number of specimens

X = mean

s = standard deviation

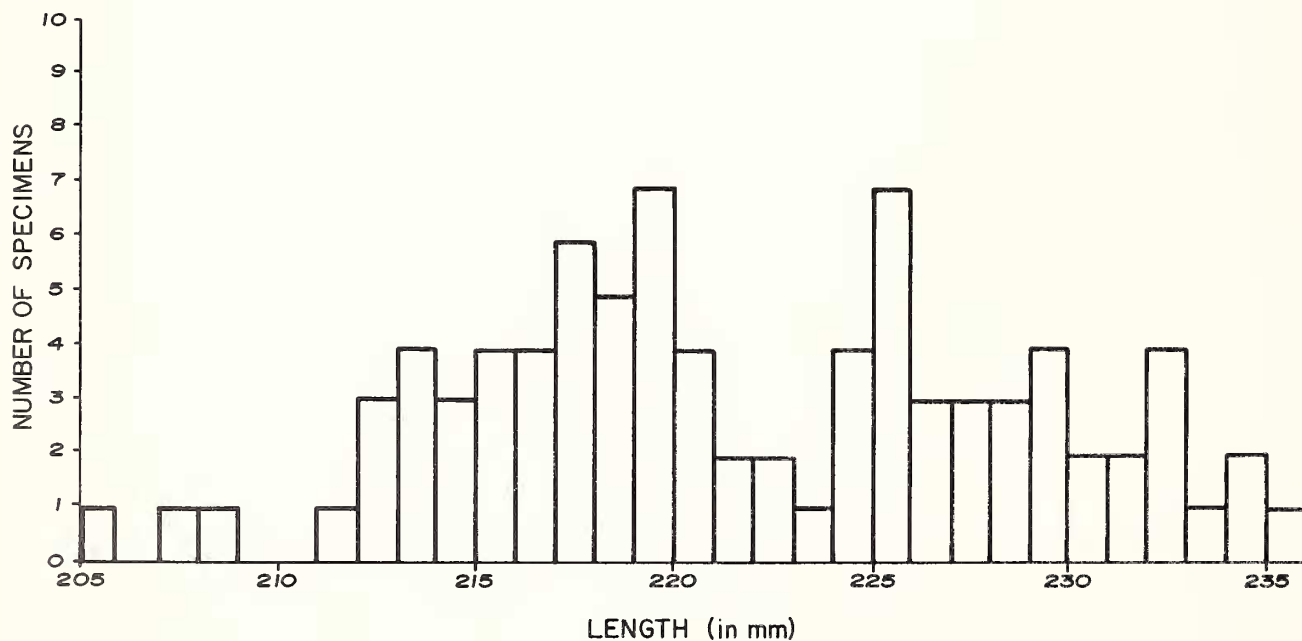


FIGURE 1. Length-frequency histogram of *Bison* metacarpals from Rancho La Brea.

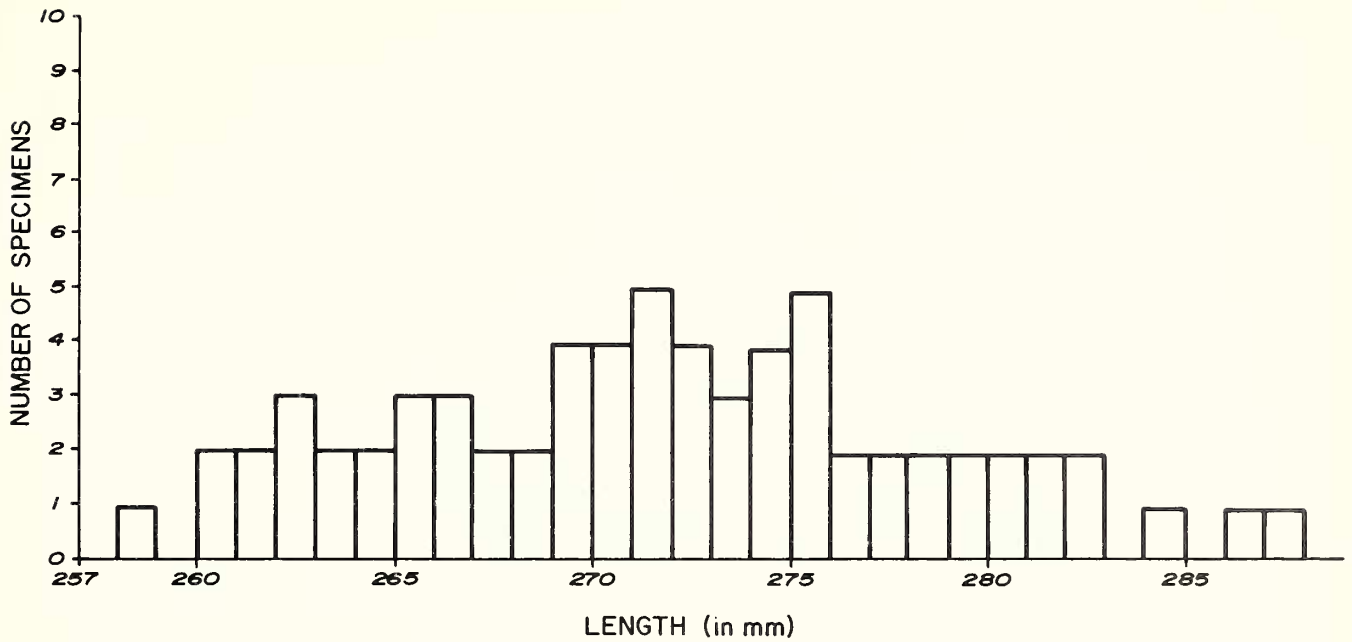


FIGURE 2. Length-frequency histogram of *Bison* metatarsals from Rancho La Brea.

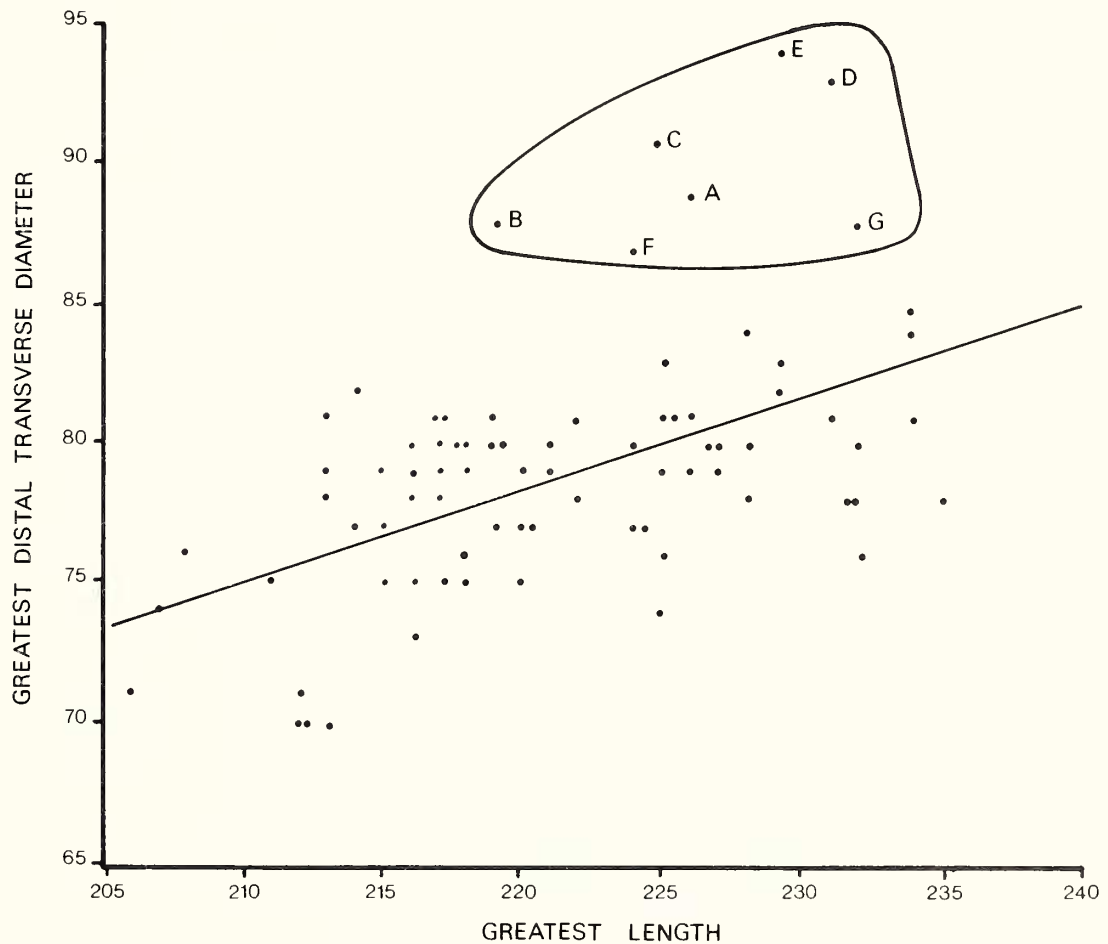


FIGURE 3. Bivariate scatter diagram of *Bison* metacarpals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

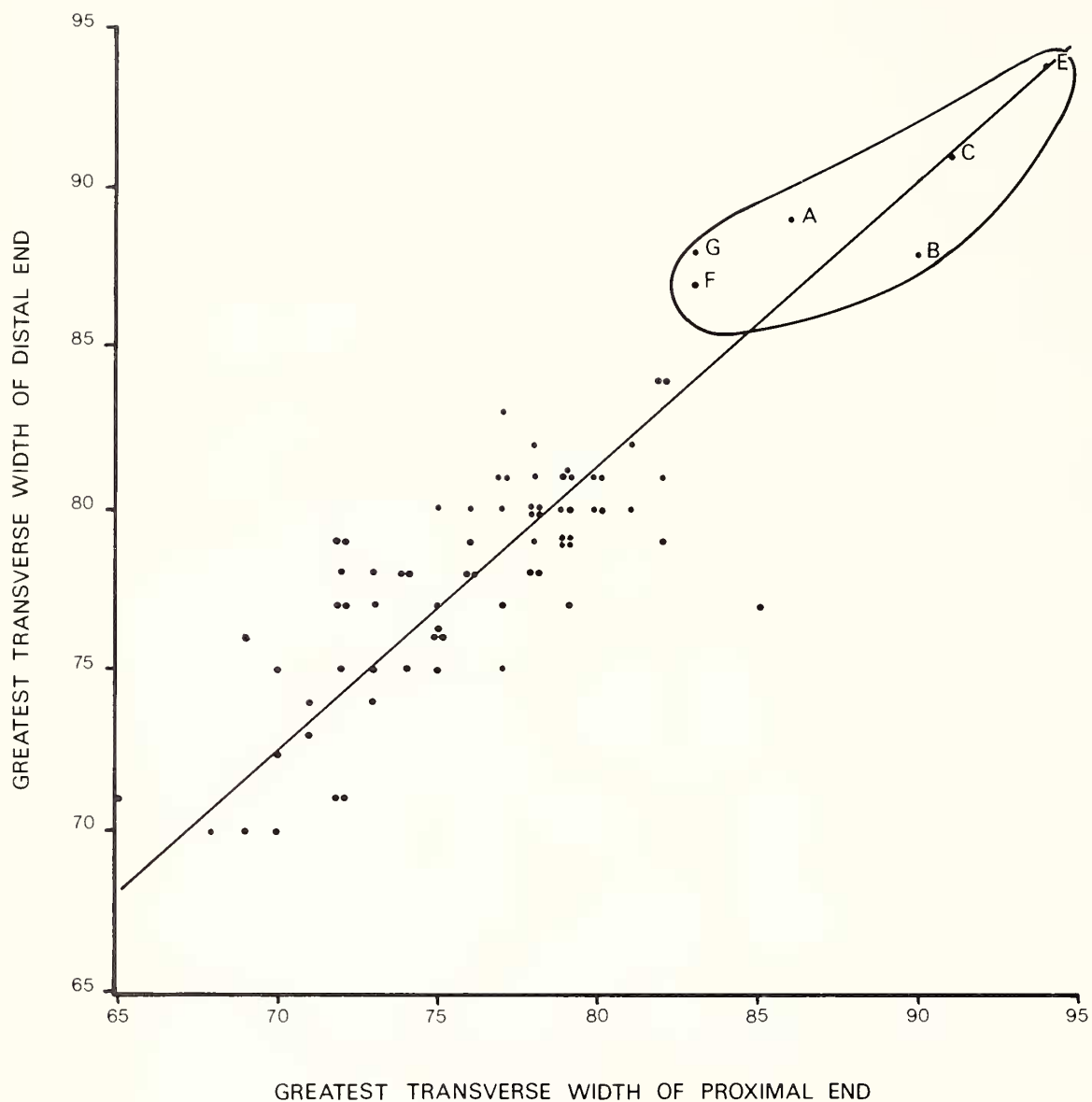


FIGURE 4. Bivariate scatter diagram of *Bison* metacarpals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

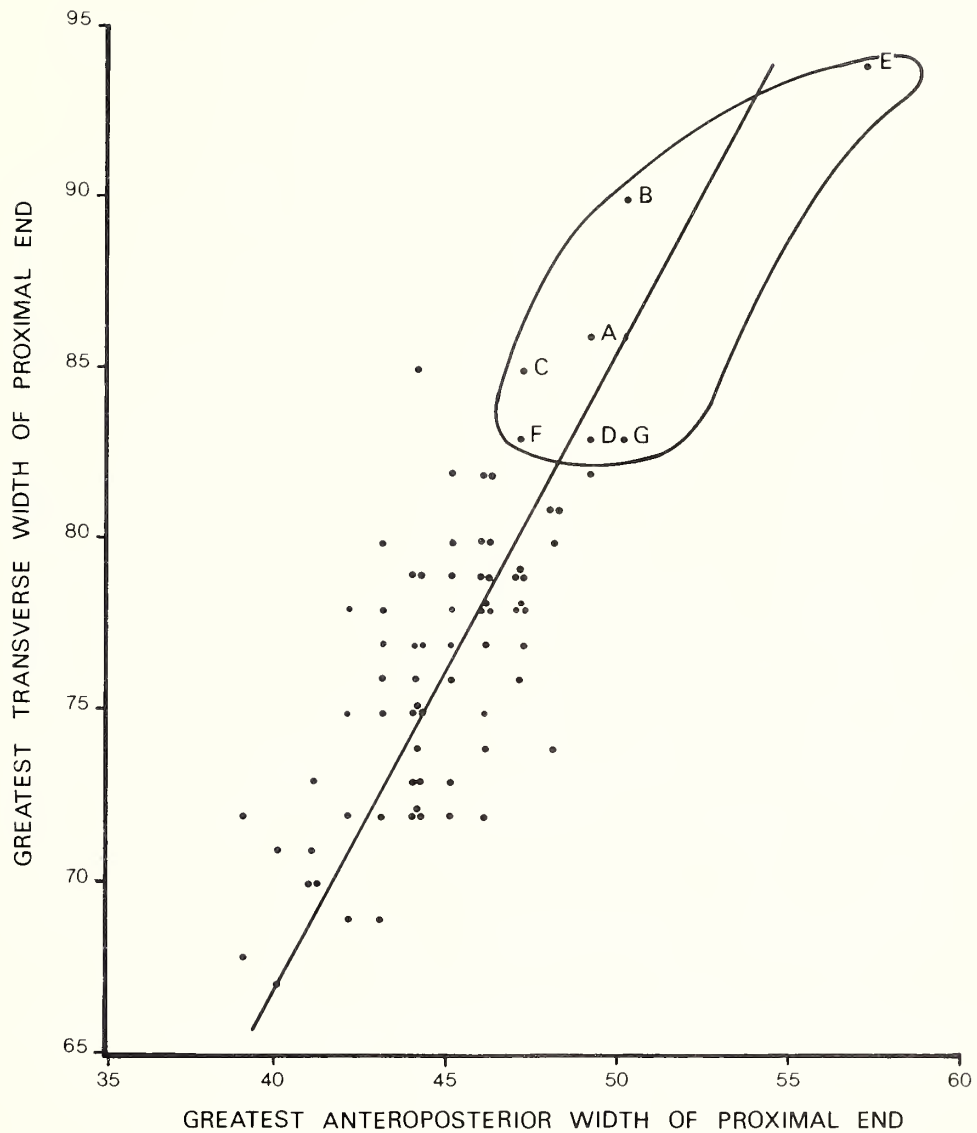


FIGURE 5. Bivariate scatter diagram of *Bison* metacarpals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

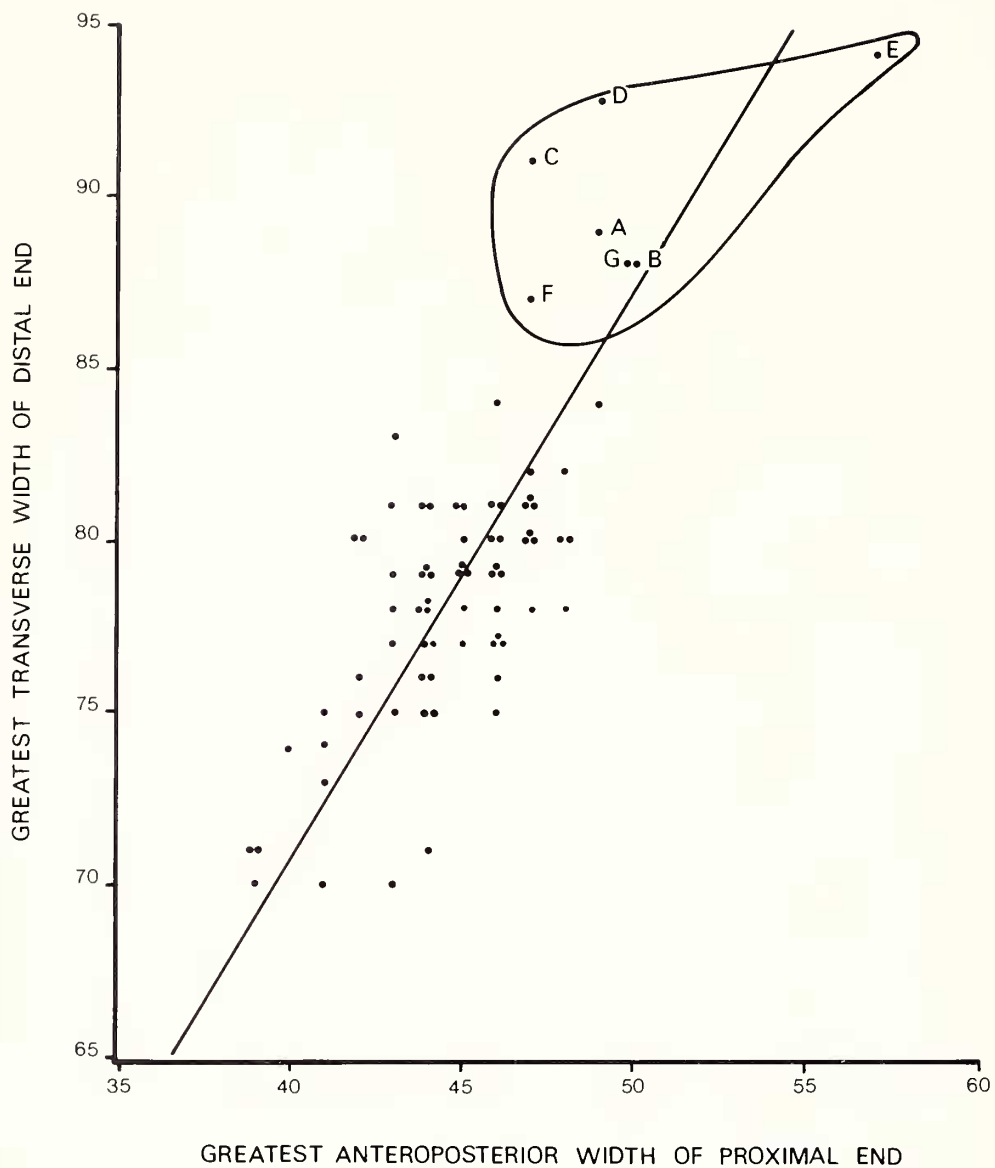


FIGURE 6. Bivariate scatter diagram of *Bison* metacarpals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

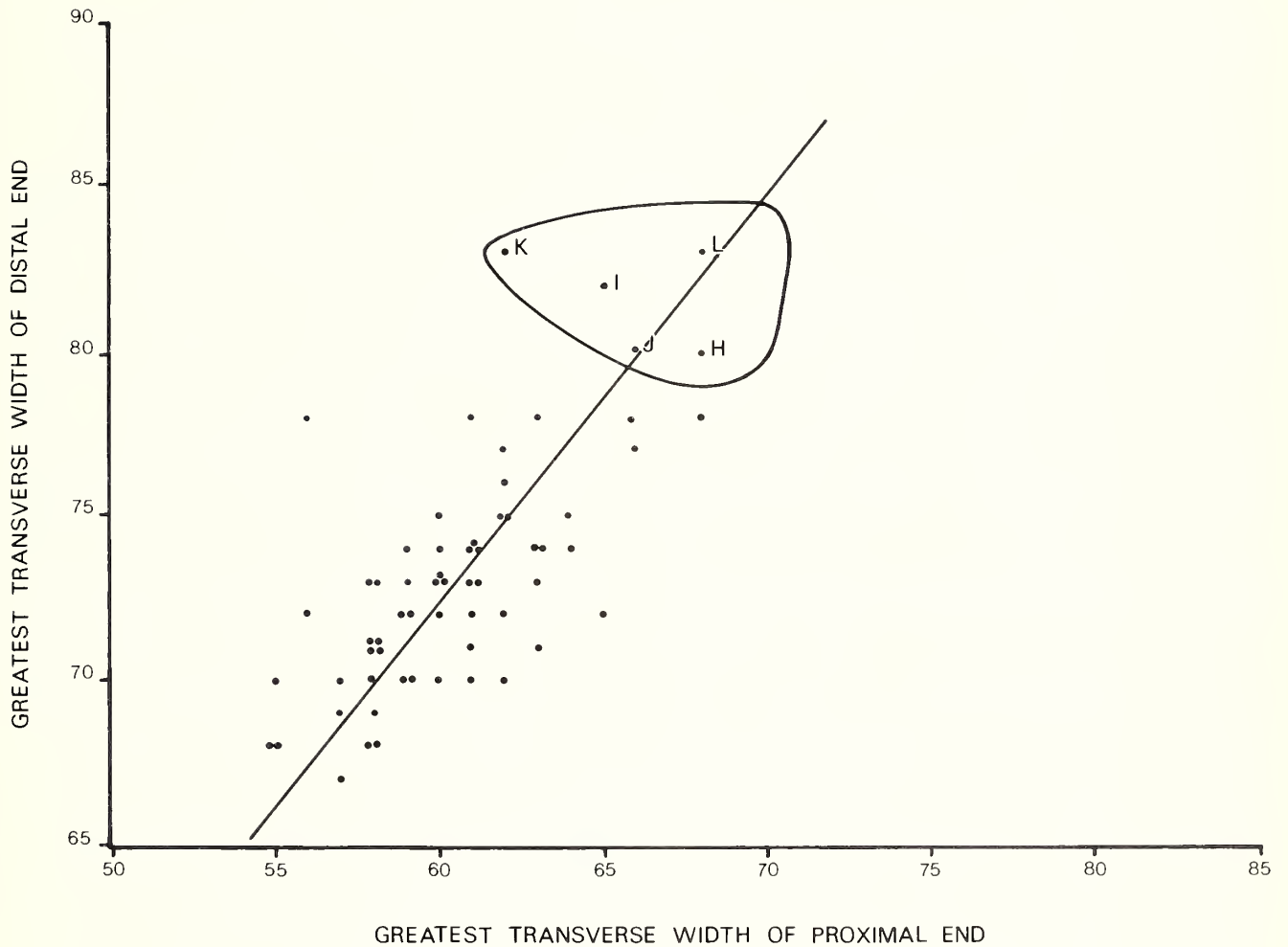


FIGURE 7. Bivariate scatter diagram of *Bison* metatarsals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

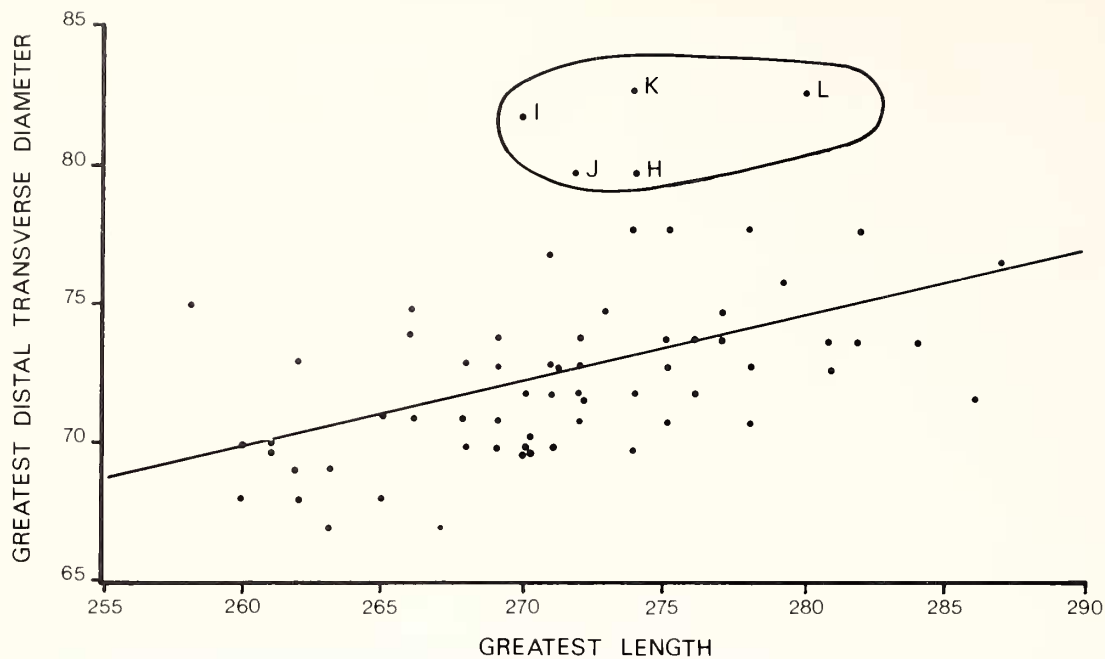


FIGURE 8. Bivariate scatter diagram of *Bison* metatarsals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

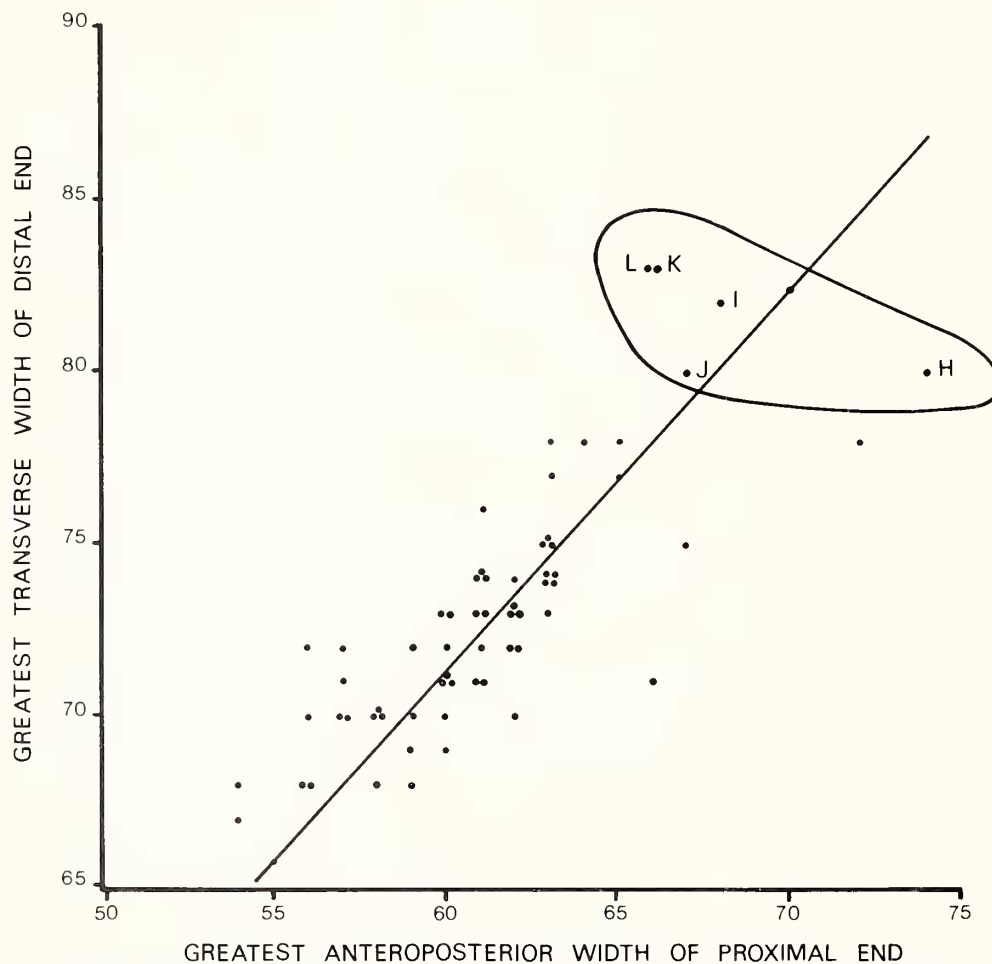


FIGURE 9. Bivariate scatter diagram of *Bison* metatarsals from Rancho La Brea (in mm). Diagonal line represents line of regression. Lettered dots found within the circle represent the same specimens on different scatter diagrams and may be indicative of *Bison latifrons*. Remaining dots mostly or completely represent *Bison antiquus*.

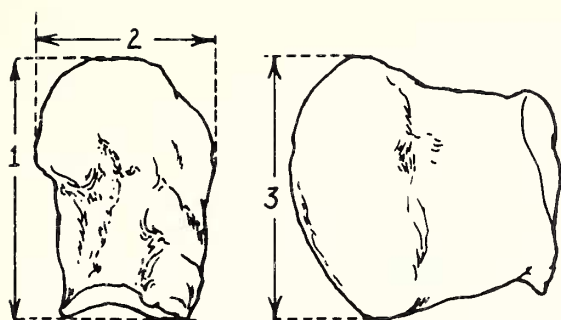


FIGURE 10. *Bison antiquus* pisiform (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

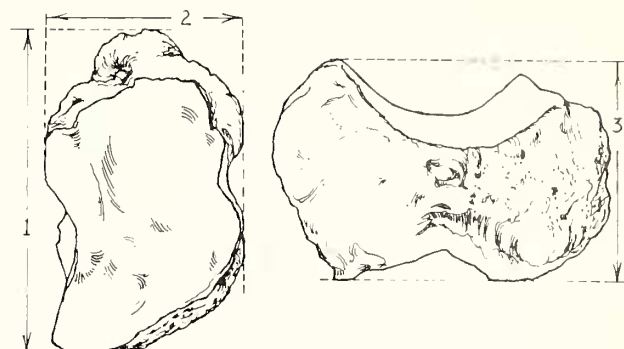


FIGURE 13. *Bison antiquus* scaphoid (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

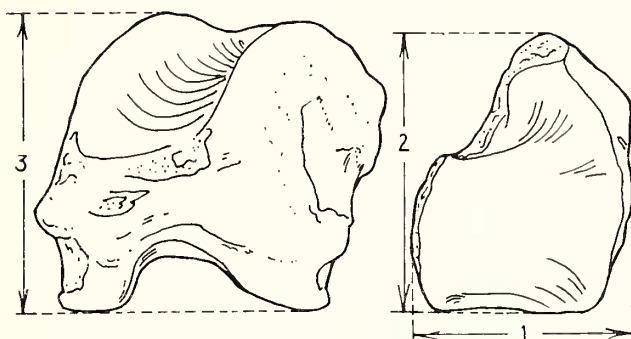


FIGURE 11. *Bison antiquus* cuneiform (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

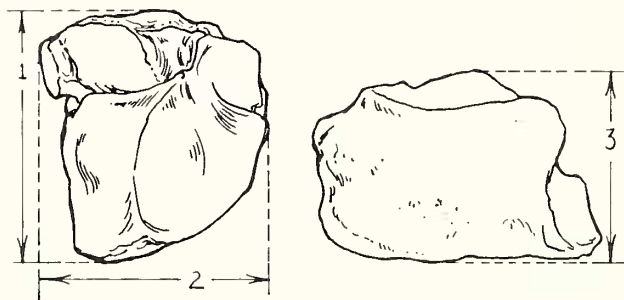


FIGURE 14. *Bison antiquus* unciform (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

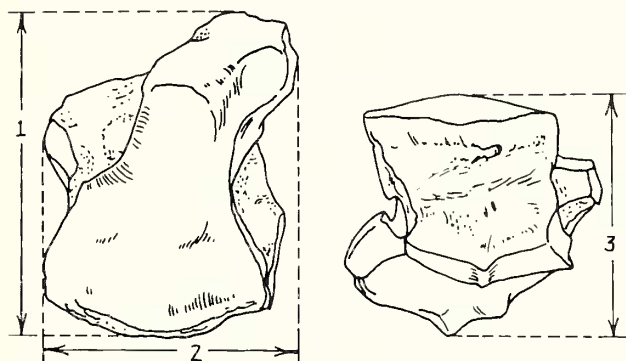


FIGURE 12. *Bison antiquus* lunar (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

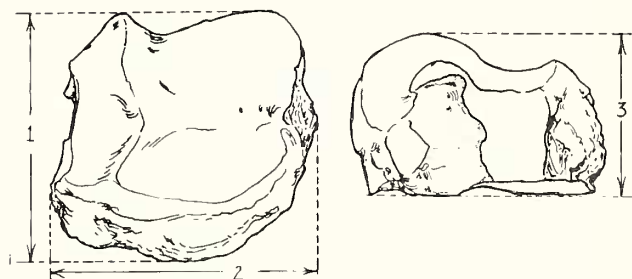


FIGURE 15. *Bison antiquus* magnum (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

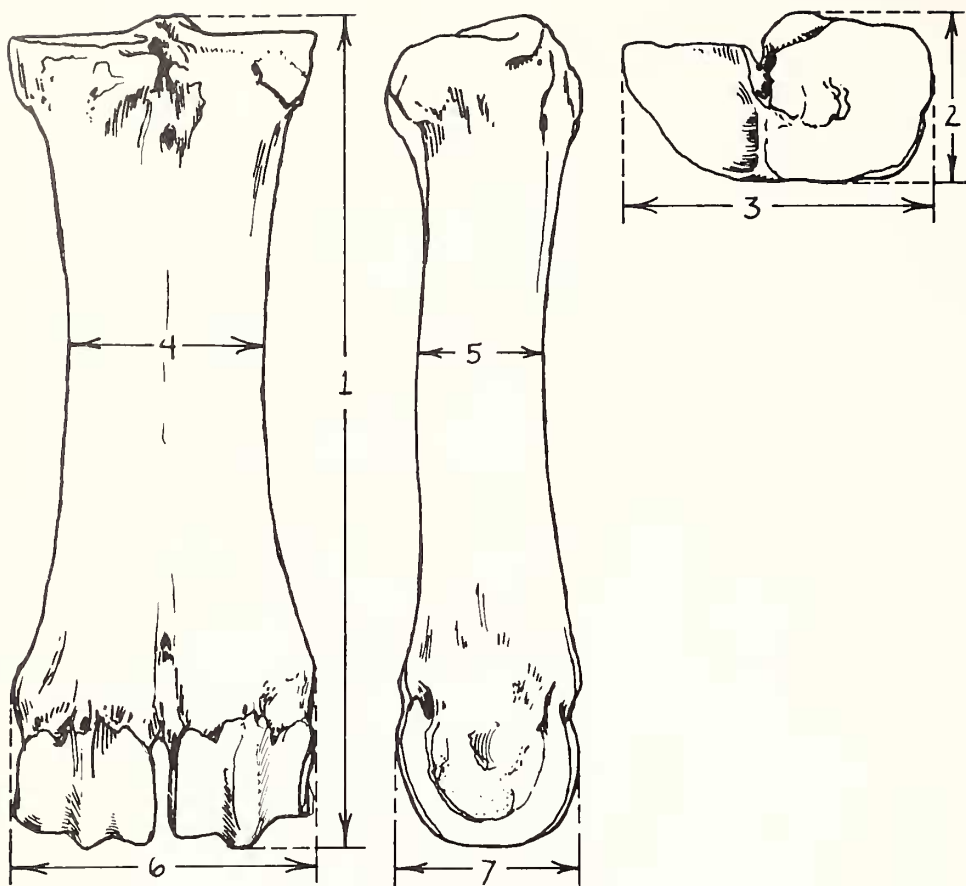


FIGURE 16. *Bison antiquus* metacarpus (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

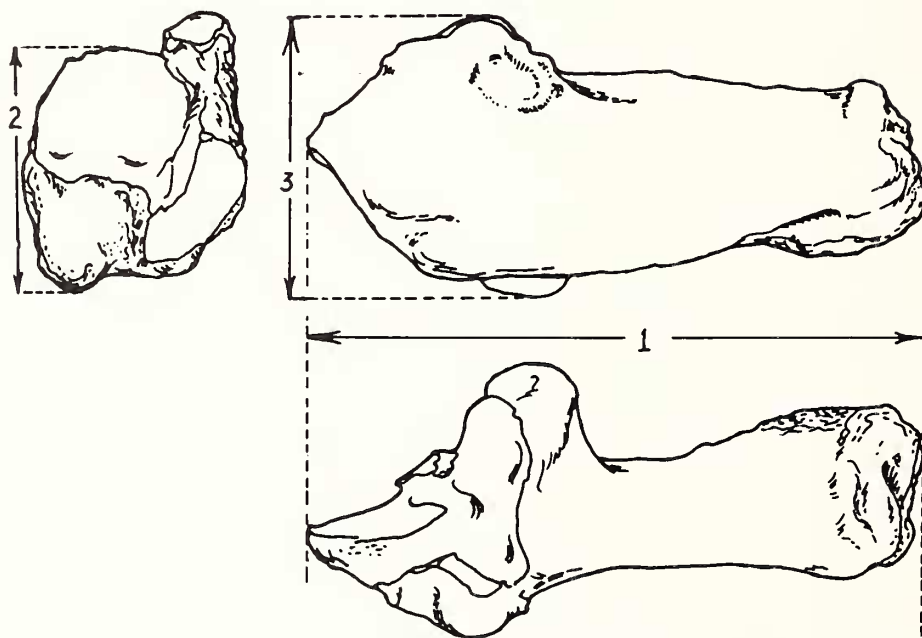


FIGURE 17. *Bison antiquus* calcaneum (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

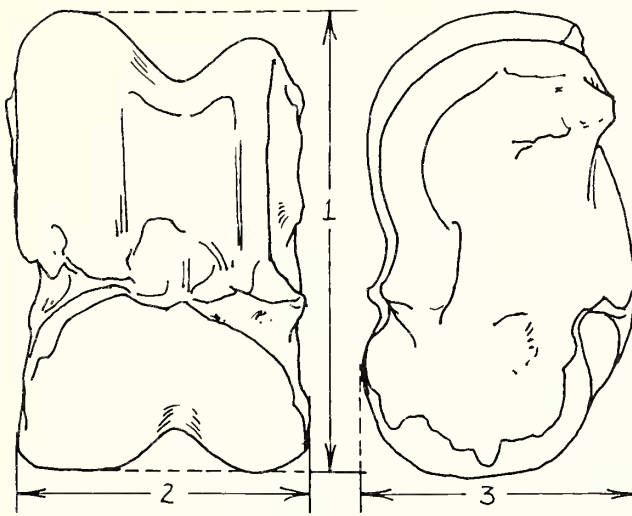


FIGURE 18. *Bison antiquus* astragalus (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

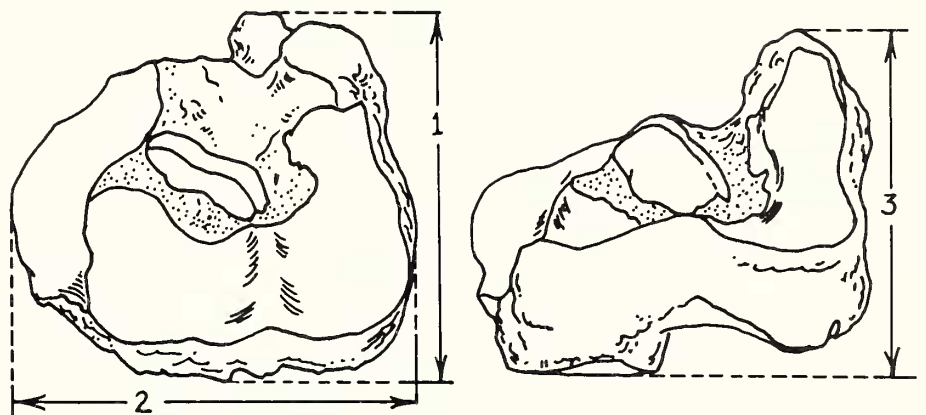


FIGURE 19. *Bison antiquus* navicular-cuboid (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

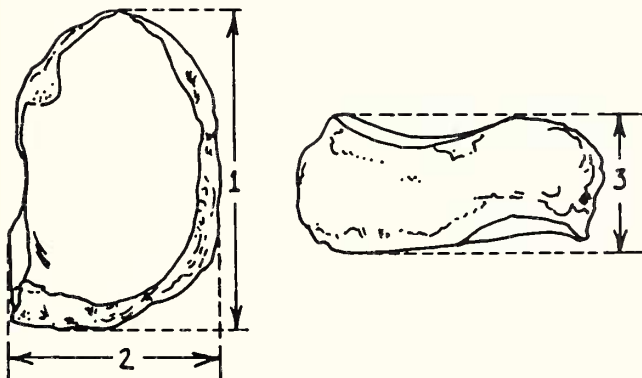


FIGURE 20. *Bison antiquus* meso-ectocuneiform (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

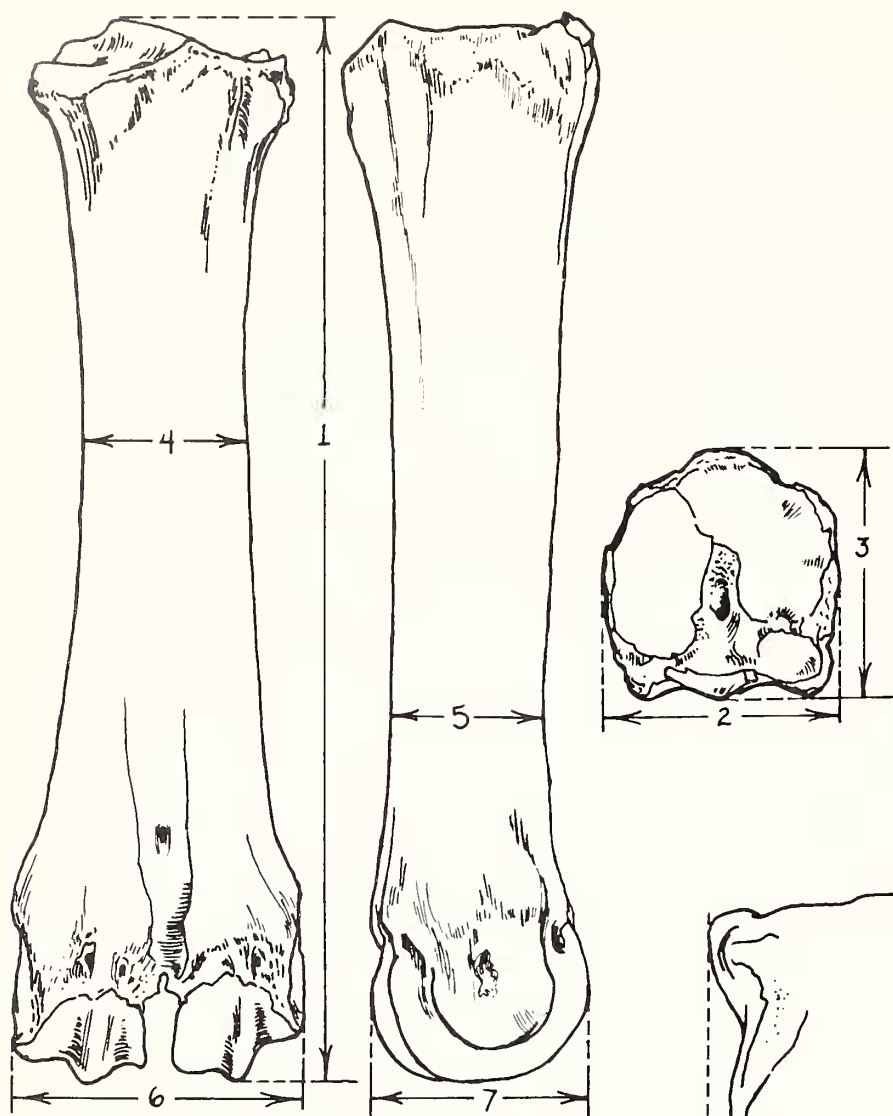


FIGURE 21. *Bison antiquus* metatarsus (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

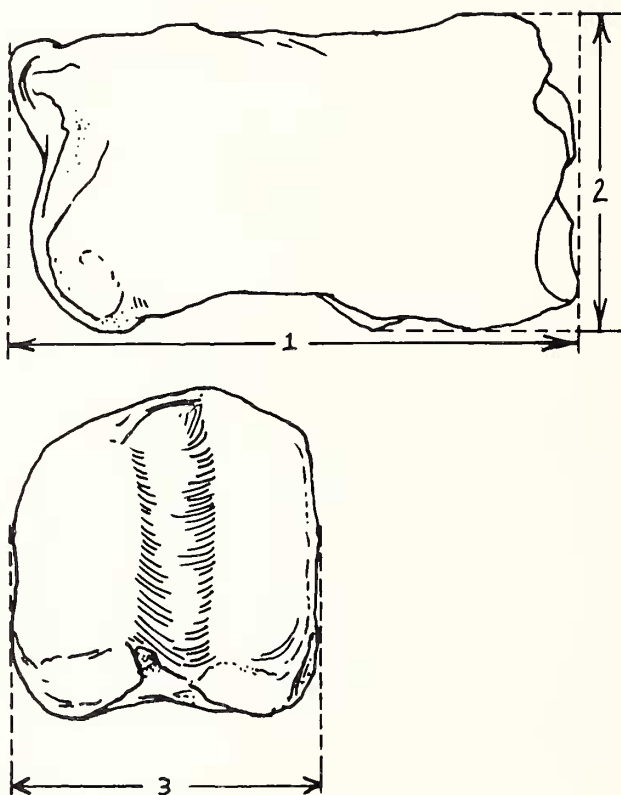


FIGURE 22. *Bison antiquus* proximal phalanx (not to scale). Numbers on drawing correspond to measurements on Table 1. Approximate measurements are given in parentheses.

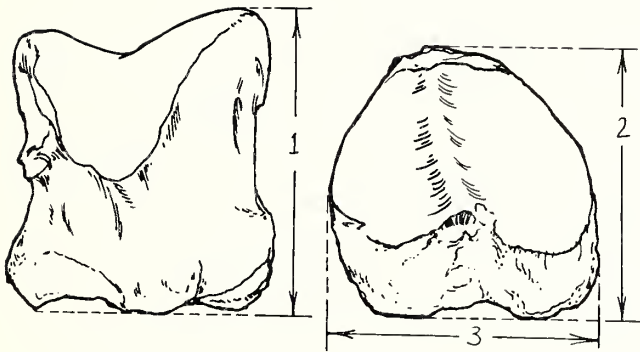


FIGURE 23. *Bison antiquus* medial phalanx (not to scale). Numbers on drawing correspond to measurements on Table I. Approximate measurements are given in parentheses.

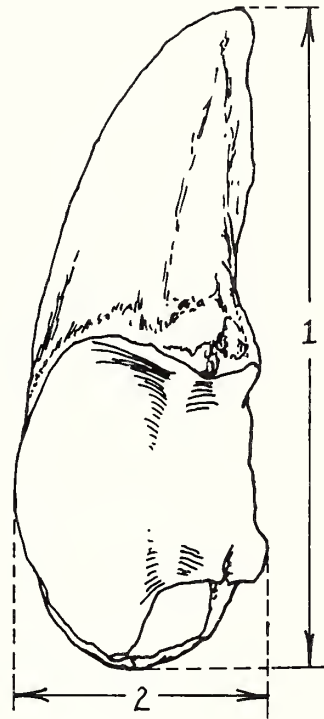


FIGURE 24. *Bison antiquus* ungual phalanx (not to scale). Numbers on drawing correspond to measurements on Table I. Approximate measurements are given in parentheses.